Spatial and Temporal Variations of Photosynthetic Parameters in Relation to Environmental Conditions in Coastal Waters of the Northern Gulf of Mexico

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ABSTRACT: On a series of eight cruises conducted in the northern Gulf of Mexico, efforts were made to characterize temporal and spatial variability in parameters of the photosynthesis-irradiance saturation curve (P^B_{max}, α^B, I_k) and to relate the observed variations to environmental conditions. Experiments to examine the importance of diel variation in upper mixed layer populations were conducted in July–August 1990 and March 1991. During July–August 1990, P^B_{max} and I_k showed significant increases and α^B decreased during the photoperiod in both river plume and shelf-slope populations. During March 1991, no consistent covariance of P-I parameters with local time was found, although highest values of α^B in the river plume were observed in early morning. Seasonal variation in P^B_{max} and α^B were correlated with temperature. Spatial variations of photosynthetic parameters in the upper mixed layer ranged from twofold to threefold within any given cruise. Variations of photosynthetic parameters in the upper mixed layer were related to principal components derived from environmental variables, including temperature, salinity, nutrients, mixed layer depth, attenuation coefficient, and daily photosynthetically available radiation (PAR). Greater than 70% of the variation in the environmental variables could be accounted for by two principal components; the majority of this variation was associated with the first principal component, which was generally strongly correlated with salinity, nutrients, mixed layer depth, and attenuation coefficient. Correlations of P^B_{max}, α^B, and I_k with the first principal component were found to be significant in some cases, an indication that spatial variability in P-I parameters was related to river outflow. Variation of P-I parameters in relation to depth and PAR were evaluated by regressions with principal components derived from depth, temperature, and mean daily PAR. For most cruises, P^B_{max} and I_k were negatively correlated with the first principal component, which was strongly positively correlated with depth and negatively correlated with daily PAR. This was consistent with a decrease in both P^B_{max} and I_k with depth that could be related to decreasing daily PAR. Positive correlations of α^B with the first principal component for two cruises, March 1991 and April 1992, indicated an increasing trend with depth. In conclusion, relationships between P-I parameters and environmental variables in the region of study were significant in some cases, but variation between cruises made it difficult to generalize. We attributed this variation to the physically dynamic characteristics of the region and the possible effects of variables that were not included in the analysis such as species composition. Our findings do support the view that a limited set of observations may be adequate to characterize P-I parameter distributions in a given region within a restricted period of time.

Introduction

Primary production in the northern Gulf of Mexico is known to be dynamic and spatially heterogeneous (Riley 1937; Thomas and Simmons

1960; Lohrenz et al. 1990; Redalje et al. 1994). This has been attributed to the strong and variable gradients in physical and chemical properties, largely a consequence of the discharge from the Mississippi and Atchafalaya rivers. The variable nature of primary production in this region has complicated
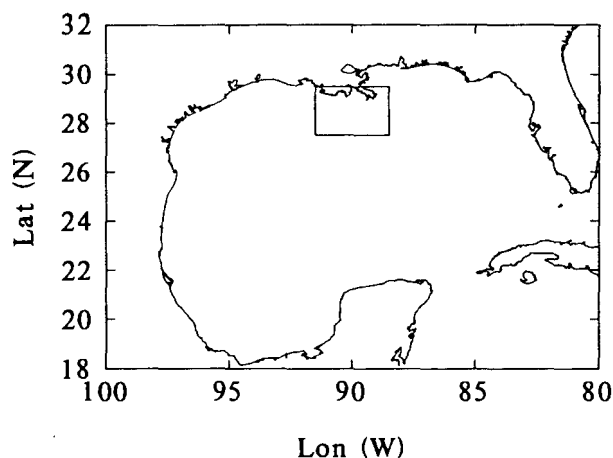
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Fig. 1. Map of the Gulf of Mexico with the study region indicated by the box.
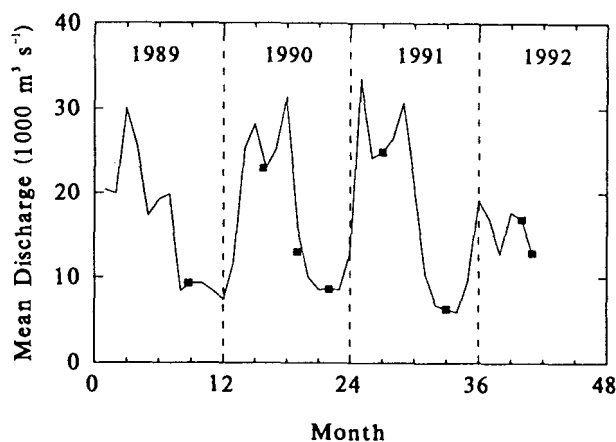

Fig. 2. Monthly mean Mississippi River discharge measured at Tarbert Landing, Mississippi. (Courtesy Army Corps of Engineers.) Symbols indicate cruise periods.

efforts to discern temporal and spatial patterns of regional productivity and their relation to possible controlling factors. Improved temporal and spatial resolution of primary production distributions has been achieved by using photosynthesis-irradiance models (e.g., Fee 1973a, b; Harrison et al. 1985). Such approaches require knowledge of the relationship of rates of pigment-specific photosynthesis to light (i.e., the photosynthesis-irradiance curve) (e.g., Jassby and Platt 1976; Platt et al. 1980). Estimates of primary production can then be made from information about biomass and irradiance distributions, thereby allowing for more detailed sampling.

Environmental variability can act at the level of physiology within phytoplankton species as well as through effects on species composition to cause variations in photosynthesis-irradiance relationships. Such variation contributes to uncertainty in estimates of primary production derived using photosynthesis-irradiance models. Previous studies have demonstrated that photosynthetic parameters may vary over a wide range of temporal and spatial scales, with temperature and light being the most commonly observed environmental covariates (Platt and Jassby 1976; Harrison and Platt 1980; Falkowski 1981; Malone and Neale 1981; Cote and Platt 1983; Harding et al. 1985; Harrison and Platt 1986). Diel periodicity (MacCaull and Platt 1977; Harding et al. 1981, 1982) and species composition and cell size (Malone and Neale 1981; Geider et al. 1986; Gallegos 1992; Gonzalez-Morales et al. 1993) have also been implicated as factors contributing to variability.

While variation in photosynthetic parameters in other coastal ecosystems has been examined, little is known about spatial and temporal variation in

the northern Gulf of Mexico. Such data can be used in the generation of modeled distributions of primary production over seasonal temporal scales and regional spatial scales (Lohrenz et al. 1992a and in preparation), and may facilitate understanding mechanisms of control at the ecosystem level. In addition, information about the distributions of photosynthesis-irradiance relationships and their responses to environmental forcing may be incorporated into larger scale predictive models of primary production (e.g., Platt and Sathyendranath 1988; Prasad et al. in press). The objectives of our study included the following: 1) characterize temporal variability of photosynthetic parameters, including diel and seasonal time scales, and 2) characterize spatial variability, including changes along vertical gradients and horizontal gradients extending from the river outflow plume, and finally, 3) relate observed variations in photosynthetic parameters to environmental conditions, where possible.

Methods

Eight cruises were conducted in the northern Gulf of Mexico at various times of the year from 1989 to 1992. Cruise dates aboard the R/V *Pelican* included September 20–27, 1989, April 23–29, 1990, October 23–29, 1990, September 12–18, 1991, April 12–19, 1992, and May 5–18, 1992. Two cruises were conducted aboard the National Oceanic and Atmospheric Administration ship *Malcom Baldrige*, July 17–August 10, 1990 and March 4–17, 1991. Sampling was generally conducted in the area of the Mississippi River delta (Fig. 1) and encompassed various stages of riverine discharge (Fig. 2). For R/V *Pelican* cruises, an instrument system was used to provide profiles of conductivity

(Seabird SBE 4-02/0), temperature (SBE 3-01/F), and pressure, depth (SBE 13-01), in situ fluorescence (SeaTech), and transmissometry (SeaTech, 5-cm path). Sensors were calibrated before and after the cruise and drift was determined to be negligible. Salinities were determined using an Autosal Model 8400. Upper mixed-layer depths were determined by visual inspection of density profiles. Samples were collected in conjunction with profiling using a rosette sampler (General Oceanics) fitted with twelve 5-l Niskin bottles. To minimize introduction of substances toxic to phytoplankton (cf. Fitzwater et al. 1982; Knauer and Martin 1983), the bottles were fitted with silicon O-rings and closure bands. Bottles were cleaned with 0.5 N Baker Instra-Analyzed HCl prior to use. During the N/S *Baldrige* cruise, samples were collected with a clean 30-l Go-Flo sampler (General Oceanics) deployed on Kevlar line and tripped with a teflon-coated messenger.

Chlorophyll *a* (Chl *a*) and phaeopigment analyses were performed on-board ship using an extraction technique modified from Shoaf and Lium (1976). Samples were filtered on Whatman GF/F glass-fiber filters, which were then immersed in 5 ml of DMSO/acetone (40/60) and allowed to extract in darkness for 1 h. After extraction, samples were centrifuged, and fluorescence was measured before and after acidification using a Turner Model 10 fluorometer (Holm-Hansen et al. 1965). Calibrations were made using a Sigma Chl *a* standard.

Nutrient analyses (NO_3^-, NO_2^-, NH_4^+, SiO_3^-, PO_4^{3-}) during the N/S *Baldrige* cruise were performed on-board using a Technicon autoanalyzer as described by Whitledge et al. (1981). For R/V *Pelican* cruises, nutrient analyses were performed on-board with an Alpkem rapid flow analyzer. The procedures of Whitledge et al. (1981) were used after conversion to small volume manifold components. Salinities were determined using an Autosal Model 8400.

Continuous measurements of surface photosynthetic photon flux density (PPFD) were recorded using a Li-Cor system, including LI-1000 data logger and an LI-190SA quantum sensor. For underwater profiling during the cruises prior to 1991, a LI-192SA underwater quantum sensor was used. During the July–August 1990 cruise, irradiance profiles were obtained using a Biospherical Instruments QSP-200 underwater quantum scalar irradiance sensor. For all subsequent cruises, a Biospherical Instruments PNF300 was used. Profiles of diffuse attenuation, $K(z)$, were computed from the measured irradiance profiles as follows:

$$K(z) = \ln[I(z_{i-1})/I(z_i)]/(z_i - z_{i-1}) \qquad (1)$$

where $I(z_i)$ is the irradiance at depth z_i. Estimates of daily PAR at depth were made by computing the attenuation of surface incident PPFD. No adjustments were made for surface reflectance.

Photosynthesis-irradiance (P-I) measurements were conducted at selected stations during each cruise. Sampling depths were generally selected to be within a range of 1–80% of surface incident irradiance. For the September 1989 cruise, P-I measurements were conducted by incubating nine small polycarbonate bottles (0.045 l) for 1 h in a gradient of sunlight attenuated to various levels with neutral density film (Rosco Sun Filters, N Series). The percentage of solar irradiance at each light level was determined by measurements obtained with a Biospherical Instruments QSL-100 equipped with a 4π sensor. The bottles were incubated in a temperature-controlled deck incubation system (cf. Lohrenz et al. 1990, 1992b). After incubation, samples were filtered onto GF/F filters using gentle vacuum (<100 mm Hg), and filters acidified with 0.5 ml 1 N HCl to eliminate inorganic ^{14}C (Lean and Burnison 1979). Filters were placed in a 20-ml scintillation vial to which 10 ml Scintiverse II (Fisher Scientific) was added.

For all subsequent cruises, photosynthesis-irradiance (P-I) measurements were conducted using a photosynthetron (e.g., Lewis and Smith 1983). Samples were inoculated with $NaH^{14}CO_3^-$ (final concentration, 10 mCi l^{-1}) and aliquots of 3 ml were dispensed into glass scintillation vials (20-ml capacity) in a temperature-controlled polyvinyl chloride block. During the October 1990 cruise, incubations of less than 1 h duration were performed using 1-ml aliquots in 7-ml scintillation vials. A range of "white" irradiance was provided with an ELH-type tungsten-halogen projection lamp directed through a heat filter of circulating water, and attenuated with neutral density screens. Quantum scalar irradiance for each vial position was measured with a Biospherical Instruments QSL-100 with a 4π collector modified to fit in the bottom half of a scintillation vial. Each P-I curve was fitted to data from 18 vial positions, with the exception of the April 1990 cruise when only nine positions were sampled for each curve. For cruises prior to 1991, total added activity was determined by subsampling a 50-μl aliquot into 4-ml Scintiverse II scintillation fluor plus 50 μl phenethylamine, 50 μl 1 M Tris-HCl, and 100 μl Milli-Q deionized water. For all subsequent cruises, a 50-μl aliquot was added to 4 ml Safety-Solve (Research Products International) containing 50 μl of a 1:1 mixture of ethanol:ethanolamine plus 50 μl 1 M Tris-HCl and 100 μl Milli-Q deionized water. Samples from the photosynthetron incubations were acidified directly (final conc. 0.3 N H_2SO_4) and purged with air for 20 min to volatilize residual $^{14}CO_2$. Prior to liq-

uid scintillation counting, 10 ml of Scintiverse II was added, with the exception that Cytoscint (ICN) was used for the April 1990 cruise samples.

Activities of productivity samples were determined by liquid scintillation analysis (Packard Tri-Carb 2000CA). Liquid scintillation counts were corrected for quenching by external standard. Dissolved inorganic carbon samples for specific activity calculations were collected in serum stoppered bottles and preserved with sodium azide (final conc. 0.001 M). Acid-volatilized CO_2 concentrations were determined by infrared absorption spectroscopy (Horriba).

The resulting photosynthetic rates, normalized to chlorophyll, were used to construct P-I curves. The P-I equation of Platt et al. (1980) was used to model the results:

$$P^B = P_s^B \cdot [1 - \exp(-\alpha^B I/P_s^B)] \cdot [\exp(-\beta^B I/P_s^B)] \tag{2}$$

where P^B (g C g Chl a^{-1} h^{-1}) is the primary production rate normalized to biomass concentration (B, mg Chl a m^{-3}), P_s^B (g C g Chl a^{-1} h^{-1}) is the saturated rate of Chl a-normalized photosynthesis in the absence of photoinhibition, α^B (g C [g Chl a h]$^{-1}$ [μmol quanta m^{-2} s^{-1}]$^{-1}$) is the initial slope of the P-I curve, β^B (g C [g Chl a h]$^{-1}$ [μmol quanta m^{-2} s^{-1}]$^{-1}$) is the parameter to characterize photoinhibition, and I (μmol quanta m^{-2} s^{-1}) is the available quantum scalar irradiance. Parameters were fit simultaneously using the NONLIN procedure of SYSTAT (Wilkinson 1990), which also produced an estimate of standard errors of the coefficients. An intercept, P_0^B (g C g Chl a^{-1} h^{-1}) was included as a parameter and checked against zero time values. In cases where differences between P_0^B and the zero time values were significant, parameters were fit using the zero time value as a constant in the equation instead of P_0^B. The maximum photosynthetic rate P_{max}^B can be computed from the following equation (Platt et al. 1980):

$$P_{max}^B = P_s^B \cdot [\alpha^B/(\alpha^B + \beta^B)] \cdot [\beta^B/(\alpha^B + \beta^B)]^{\beta/\alpha} \tag{3}$$

For simplicity of notation, the B superscripts were omitted in the exponent. Note that as β^B approaches zero, P_{max}^B approaches P_s^B.

To assess the variance in parameter estimates, two similarly constructed photosynthetrons were used during the April 1992 cruise to conduct 14 sets of parallel incubations of duplicate subsamples representative of a range of water types. P-I parameters were estimated from data collected with each incubator and were compared. Average coefficients of variation were 11% (range 1.5–29%) for P_{max}^B, 15% (range 5.1–36%) for α^B, and 40% (range 6–96%) for β^B. A comparison was also made be-

tween the tube incubation method as used on the September 1989 cruise and the photosynthetron method as used on subsequent cruises. Results obtained with the tube incubation method were found to be 30–32% lower for P_{max}^B, while values of α^B ranged from 11% above to 45% below values obtained with the photosynthetron method (data not shown). Values of β^B were not significantly different from zero, so a comparison was not possible. One explanation for the offset in P_{max}^B was that the filtration procedure used with the tube incubation method would not have included recently fixed dissolved organic carbon released from phytoplankton during the incubation or lost as a result of filtration. Because the range of variability between cruises was greater than these methodological differences, we made no effort to adjust the September 1989 data.

Experiments were conducted to evaluate diel periodicity during the July–August 1990 and March 1991 cruises. Samples were collected in early morning and held in clean polycarbonate bottles in a temperature-controlled deck incubation system adjusted to simulate in situ irradiance (cf. Lohrenz et al. 1990, 1992b). Subsamples for Chl a and P-I determinations were removed at various times during the day. An alternative strategy to evaluate diel variations was to sample periodically in the vicinity of a drifting sediment trap array (cf. Redalje et al. 1994). During March 1991, in addition to these methods, we also sampled at various times of day while anchored at a station in the Mississippi River plume.

During the July–August 1990 cruise, determinations were also made of carbon-specific growth rates and carbon biomass (labeled Chl a technique; Redalje and Laws 1981; Redalje 1983; Redalje 1993). Briefly, samples were incubated in 1-l polycarbonate bottles under simulated in situ conditions for 24 h. After incubation, samples were filtered onto GF/F filters using gentle vacuum, and stored in liquid N_2 for postcruise processing. Samples were processed as described in Redalje (1993).

Results

DIEL VARIATION

During July–August 1990, a consistent pattern of diel variation was observed (Table 1 and Fig. 3). Lowest values of P_{max}^B and highest values of α^B occurred in the early morning in both river plume and shelf, slope populations. Analysis of covariance (SYSTAT, Wilkinson 1990) of P-I data from the July–August cruise provided evidence for a significant increase in P_{max}^B and a decrease in α^B with local time in both plume and shelf populations (Fig. 3). The asynchronous variation in P_{max}^B and α^B led to the result that the light saturation parameter, I_k (=

TABLE 1. Diel variation in upper-mixed-layer photosynthetic parameters during July–August 1990. Units are as follows: P^B_{max} (g C g Chl a^{-1} h^{-1}), α^B (g C [g Chl a h]$^{-1}$ [μmol quanta m^{-2} s^{-1}]$^{-1}$), I_k (μmol quanta m^{-2} s^{-1}). SE = standard error of the estimate.

Conditions	Latitude (N)	Longitude (W)	Date	Local Time (h)	P^B_{max}	SE	α^B	SE	I_k
Incubated samples									
Plume	28.912	89.490	July 22, 1990	7.3	6.0	0.6	0.026	0.003	236
				11.7	22.1	0.7	0.021	0.001	1031
				18.8	12.4	0.8	0.030	0.003	416
Shelf	28.643	90.463	July 30, 1990	6.4	6.0	0.3	0.045	0.003	133
				11.8	8.6	0.4	0.035	0.001	248
				16.8	7.7	0.4	0.031	0.001	249
Shelf	28.900	89.942	August 1, 1990	6.0	5.2	0.2	0.040	0.002	132
				12.0	6.0	0.2	0.026	0.002	234
				17.0	7.1	0.4	0.027	0.001	258
Slope	27.762	90.032	August 5, 1990	6.5	3.0	0.4	0.016	0.005	184
				12.0	7.3	0.8	0.009	0.001	843
				17.1	10.5	2.6	0.008	0.002	1268
Drifter stations									
Plume	28.820	89.578	July 25, 1990	5.3	8.3	0.7	0.042	0.003	197
Plume	28.780	89.606	July 25, 1990	12.6	12.7	0.3	0.043	0.002	298
Plume	28.743	89.636	July 25, 1990	15.4	11.9	0.9	0.037	0.002	323
Plume	28.710	89.672	July 25, 1990	18.3	12.1	1.1	0.042	0.002	286
Plume	28.722	89.783	July 26, 1990	6.0	6.7	0.4	0.041	0.002	165
Plume	28.703	89.835	July 26, 1990	12.6	10.9	0.7	0.042	0.002	261
Plume	28.683	89.910	July 26, 1990	18.0	9.6	0.6	0.037	0.002	259
Shelf	28.700	90.317	August 2, 1990	9.6	8.0	0.6	0.037	0.003	219
Shelf	28.679	90.308	August 2, 1990	12.8	6.1	0.5	0.024	0.002	253
Shelf	28.681	90.322	August 2, 1990	17.9	6.5	0.5	0.029	0.002	228
Shelf	28.819	90.303	August 3, 1990	6.1	5.0	0.3	0.040	0.004	124

P^B_{max}/α^B), increased during the photoperiod (Table 1 and Fig. 3). During March 1991, no significant covariance was found between any of the parameters and local time (Fig. 4), although values of α^B in plume waters were again highest in early morning (Table 2 and Fig. 4).

SEASONAL VARIATION

Seasonal variation was evident from a comparison of means of midday (1000–1400 local time) values of P^B_{max}, α^B, and I_k (Table 3). Some of the variation could be related to changes in temperature. Highest mean values of P^B_{max}, α^B, and I_k were observed during the September 1991 cruise (Table 3), during which some of the highest water temperatures (28–30°C) were observed. Lowest mean values of P^B_{max} and α^B were observed during March 1991, the period in this study when lowest temperatures were observed (9–20°C). An analysis of the combined P-I data from all cruises showed that both P^B_{max} and α^B were significantly correlated with temperature, although there was considerable scatter in the data (Fig. 5). Highest values of P^B_{max} fit an exponential relationship with temperature.

HORIZONTAL SPATIAL VARIATION

Horizontal spatial variations of P^B_{max} and α^B in the upper mixed layer ranged from twofold to threefold within any given cruise as illustrated by plot-

ting values in relation to salinity (Figs. 6 and 7). In some cases, this variation could be related to effects of river outflow. For example, analysis of covariance of P-I data from July–August 1990 indicated that adjusted means of P^B_{max} and I_k in the river plume were significantly higher than in shelf populations (Fig. 3). This coincided with higher observed phytoplankton carbon-specific growth rates in the plume region (Fig. 8). In contrast, no significant regional differences in α^B could be demonstrated (Fig. 3), nor was there any apparent relationship between α^B and growth rate (Fig. 8). Analysis of variance of P-I data from March 1991 indicated that the adjusted mean of P^B_{max} in the river plume was significantly lower than in shelf waters (Fig. 4), a finding opposite of that for July–August 1990. Analyses of variance of α^B and I_k revealed no significant differences between plume and shelf populations at that time (Fig. 4).

In an effort to identify associations between the observed spatial variations and environmental conditions, we examined relationships of photosynthetic parameters to principal components derived from environmental variables. To minimize the influence of diel variation, only data collected during midday (1000–1400 hours) were used. Variables included in the analysis were the following: temperature, salinity, silicate, phosphate, nitrate + nitrite, attenuation coefficient for downwelling PAR,
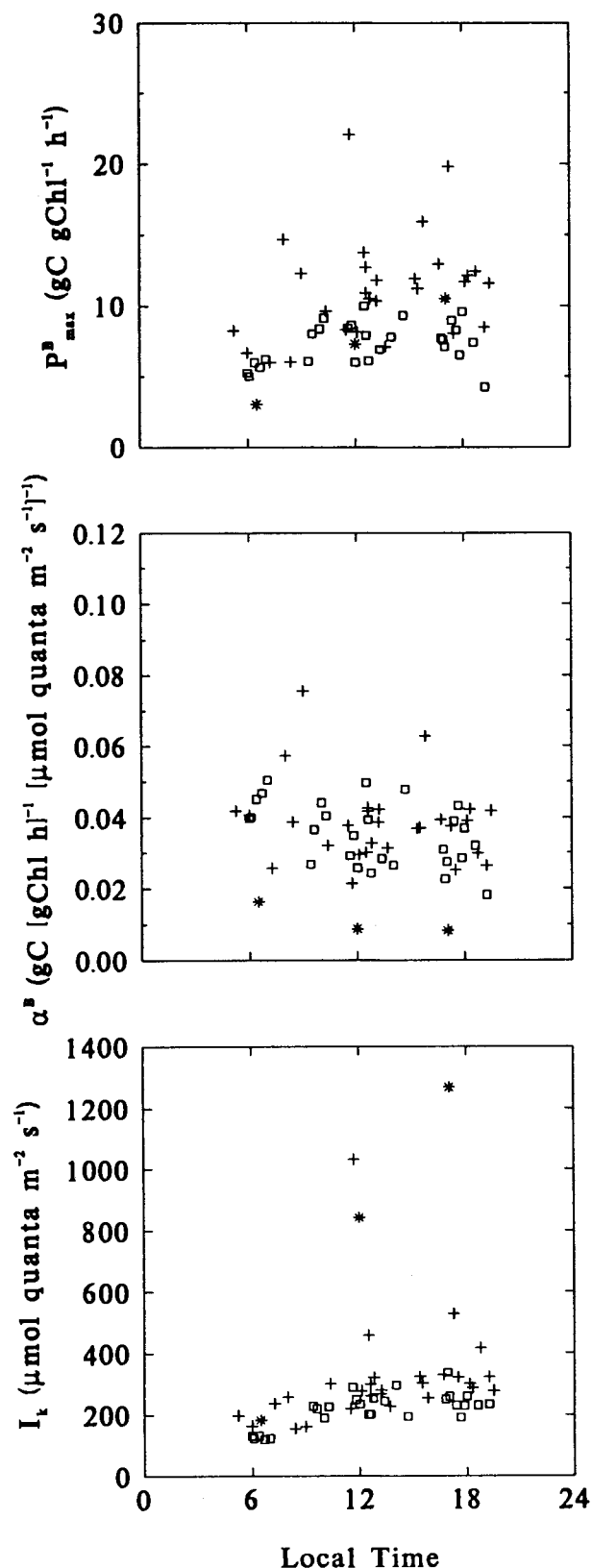
mixed layer depth, and daily PAR at depth. Prior to analysis, data were transformed to natural logarithms to equalize variances. Principal component analysis was performed using the FACTOR procedure of SYSTAT (Wilkinson 1990). The procedure involved construction of a correlation matrix using pairwise deletion from which principal components were subsequently derived. For some of the cruises, certain variables were omitted because of insufficient data. An examination of component loadings (equivalent to correlation coefficients with original variables) revealed similarities between the components derived for the different cruises (Table 4). Generally, it was found that more than 70% of the variation in the environmental data could be accounted for by the first two principal components (Table 4); the majority of this variation was described by the first principal component, which generally showed strong negative correlations with salinity and mixed layer depth and positive correlations with nutrients and attenuation coefficient. Relationships of temperature and daily PAR with the first principal component were more variable. Temperature showed a strong positive correlation with the first component in April 1990 and with the second component in September 1989, April 1992, and May 1992. A strong negative correlation was observed between temperature and the second principal component in July–August 1990, while daily PAR displayed a positive relationship with the second principal component throughout all cruises.

Relationships between the principal components' variables and midday values of P^B_{max}, α^B, and I_k were analyzed using stepwise multiple regression (SYSTAT, Wilkinson 1990) and were found to be significant in some cases (Tables 5 and 6). Probability thresholds were set at 0.15 for entrance or removal of principal components as predictors in the stepwise regression models. The value of 0.15 is valid for independent predictors as shown by Monte Carlo studies of stepwise regression (Bendel and Afifi 1977). The relationships between P-I parameters and the first principal component were found to differ between cruises. P^B_{max} was positively correlated with the first principal component (i.e.,

Fig. 3. Values of P-I parameters during July–August 1990 as a function of local time. Symbols indicate different locations as follows: +, river plume; □, shelf; *, slope. Analysis of covariance of the plume and shelf data (n = 55) revealed a significant effect of local time on the values of P^B_{max} (p = 0.012), α^B (p = 0.017), and I_k (p < 0.001). The analysis also indicated adjusted means of P^B_{max} and I_k were significantly higher in the plume than in shelf waters (p < 0.001 for both), even when the highest data points from each were omitted.

TABLE 2. Diel variation in the upper-mixed-layer photosynthetic parameters during March 1991. Units are as follows: P^B_{max} (g C g Chl a^{-1} h^{-1}), α^B (g C [g Chl a h]$^{-1}$ [μmol quanta m^{-2} s^{-1}]$^{-1}$), I_k (μmol quanta m^{-2} s^{-1}). SE = standard error of the estimate.

Conditions	Latitude (N)	Longitude (W)	Date	Local Time (h)	P^B_{max}	SE	α^B	SE	I_k
Incubated samples									
Plume	28.913	89.563	March 6, 1991	6.3	5.2	0.5	0.022	0.004	234
				10.6	5.1	0.4	0.011	0.002	447
				15.6	3.9	0.4	0.014	0.004	276
Shelf	28.754	90.139	March 11, 1991	6.4	3.5	0.8	0.014	0.006	252
				10.5	9.2	3.7	0.013	0.002	712
				15.3	10.3	1.7	0.019	0.004	529
Slope	28.235	88.796	March 15, 1991	7.1	4.1	1.3	0.015	0.005	268
				11.7	8.0	0.7	0.031	0.007	255
				14.8	8.7	1.8	0.024	0.005	366
Anchor station									
Plume	28.910	89.491	March 14, 1991	5.7	4.7	0.3	0.031	0.005	153
Plume	28.910	89.494	March 14, 1991	8.8	4.3	0.3	0.025	0.004	170
Plume	28.908	89.491	March 14, 1991	12.4	4.3	0.3	0.014	0.002	307
Plume	28.909	89.490	March 14, 1991	15.9	5.9	1.5	0.017	0.003	338
Drifter stations									
Plume	28.844	89.616	March 8, 1991	6.1	2.7	0.2	0.012	0.002	222
Plume	28.886	89.631	March 8, 1991	11.1	1.8	0.1	0.007	0.001	247
Shelf	28.613	90.227	March 12, 1991	7.3	5.6	0.5	0.026	0.004	220
Shelf	28.706	90.249	March 12, 1991	12.4	5.4	0.5	0.029	0.007	187

inversely related to salinity) in July–August 1990 and April 1992, and it was negatively correlated with the first principal component in March 1991 (Table 5). A positive correlation was found for α^B with the first principal component for April 1990, and a negative association was found for March 1991. I_k was found to be negatively correlated with the first principal component in September 1989 and April 1990 (Table 6). Significant correlations between P-I parameters and the second component were always of the same sign; P^B_{max} was positively correlated with the second principal component in July–August 1990 and September 1991, while α^B was negatively correlated with the second principal component in July–August 1990, April 1992, and May 1992 (Table 5). I_k was found to be positively correlated with the second principal component in July–August 1990, September 1991, and April and May 1992 (Table 6).

VERTICAL VARIATION

P-I parameter data from all depths were related to principal components that had been derived from depth, temperature, and mean daily photosynthetically active radiation (PAR) variables. Again, only midday values were used in the analysis. For all cruises, it was found that the first principal component exhibited strong positive associations with depth and negative associations with PAR, while associations with temperature varied (Table 7). For several cruises, P^B_{max} and I_k were found to be negatively correlated with the first component (Tables 6 and 8), a result that was in-

terpreted to reflect a depth-dependent decrease in these parameters. Correlations of α^B with the first component were positive and significant only in March 1991 and April 1992 (Table 8). The second principal component was consistently positively associated with temperature, while exhibiting weak and variable relationships to depth and daily PAR. Both positive and negative correlations of parameters with the second principal component were observed. One possible interpretation was that the second principal component described variation related to horizontal differences between water masses (e.g., phytoplankton species composition, nutrient availability, temperature, light history).

Discussion
DIEL VARIATION

The observation that P^B_{max} and I_k increased over the photoperiod during July–August 1990 (Table 1 and Fig. 3) was consistent with previously reported observations for both coastal and offshore phytoplankton assemblages (MacCaull and Platt 1977; Kana et al. 1985). Diel periodicity has been attributed to a combination of endogenous physiological oscillations as well as responses to environmental light cues (e.g., MacCaull and Platt 1977; Falkowski 1984). Our findings differed from some earlier work (Harding et al. 1981, 1982) in that we observed a diel periodicity in α^B that was out of phase with that of P^B_{max} (i.e., α^B tended to be higher in early morning samples). It is possible that phytoplankton assemblages in this northern Gulf of Mexico region exhibit physiological characteristics
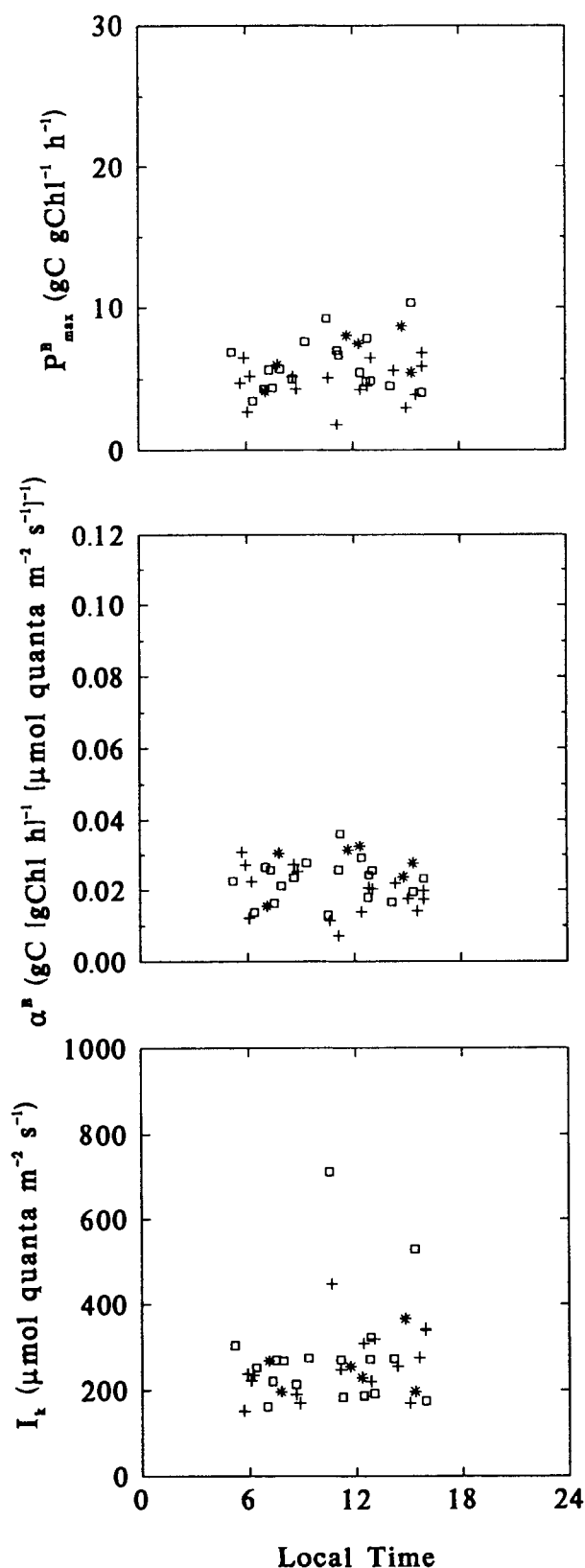
distinct from those previously studied, perhaps due in part to the fact that our study area was characterized by complex and dynamic environmental conditions. Our results may also have been influenced by the temporal coverage of our sampling, which was limited only to the photoperiod, that being the time of day relevant to calculations of primary production.

Changes in photosynthetic parameters are believed to represent a combination of relatively short-term responses typical of light harvesting and electron transport processes as well as more long-term processes typical of changes in enzymatic activity and turnover or synthesis of cellular constituents (Falkowski 1981, 1984, 1992; Neale and Marra 1985). Photosynthetic mechanisms that could lead to inverse diel changes in P^B_{max} and α^B can be explored on the basis of theoretical arguments. The following expression can be used to approximate light-saturated photosynthesis:

$$P^B_{max} = \eta/\tau \tag{4}$$

where η (mol O_2 mol Chl a^{-1}) corresponds to the ratio of functional photosystem 2 reaction centers (i.e., oxygen-evolving units) to Chl a, and τ is the turnover time for electrons to flow through the photosynthetic electron-transport chain from water to carbon dioxide (Falkowski 1981, 1992). The initial slope of the P-I curve (α^B), and can be expressed as the following:

$$\alpha^B = \eta\sigma \tag{5}$$

where σ (m^2 quanta^{-1}) is the functional absorption cross-section of photosystem 2, that entity involved with production of O_2 (Ley and Mauzerall 1982). Note that this term is distinct from the optical absorption cross section (cf. Dubinsky 1992; Falkowski 1992). From Eqs. 4 and 5, it can be seen that I_k may be expressed as follows:

$$I_k = 1/\sigma\tau \tag{6}$$

The parameter I_k, defined by Talling (1957), has been cited as an indicator of photoadaptive responses to changes in the photic environment. Studies with cultured phytoplankton have shown that σ may decrease on time scales of minutes (state transitions) to hours (photoadaptation) in response to increased irradiance (Falkowski 1992).

←

Fig. 4. Values of P-I parameters during March 1991 as a function of local time (+, river plume; □, shelf; *, slope). Analysis of covariance of the plume and shelf data (n = 34) showed no significant effect of local time on the values of P^B_{max} (p = 0.461), α^B (p = 0.467), or I_k (p = 0.151). The analysis did reveal that adjusted means of P^B_{max} were significantly lower in the plume than in shelf waters (p = 0.035).

TABLE 3. Means and standard deviations (SD) of midday (1000–1400 hours) values of photosynthetic parameters in the upper mixed layer. Units are as follows: P^B_{max} (g C g Chl a^{-1} h^{-1}), α^B (g C [g Chl a h]$^{-1}$ [μmol quanta m^{-2} $s^{-1}]^{-1}$), I_k (μmol quanta m^{-2} s^{-1}). n = number of samples.

Cruise	P^B_{max}		α^B		I_k		
	Mean	SD	Mean	SD	Mean	SD	n
September 1989	9.0	3.6	0.032	0.010	284	59	9
April 1990	10.4	3.4	0.041	0.014	281	127	7
July–August 1990	10.0	3.8	0.033	0.010	349	231	17
October 1990	11.3	5.3	0.049	0.024	246	74	10
March 1991	6.1	2.0	0.022	0.009	303	142	13
September 1991	23.0	5.5	0.055	0.015	429	83	7
April 1992	8.4	2.3	0.028	0.011	370	213	16
May 1992	5.4	2.8	0.018	0.004	325	221	5

τ has also been shown to decrease with increasing growth irradiance (e.g., Sukenik et al. 1987) and appears to be influenced by Calvin-cycle processes (Falkowski 1992). Such changes would be consistent with diel increases in P^B_{max} and I_k and decreases in α^B observed during July–August 1990. Functional changes in η have been attributed to photoinhibition or nutrient limitation (Falkowski 1992; Kolber and Falkowski 1993), and such changes may have been a mitigating factor in the diel patterns we observed.

There was no discernable diel pattern in P-I parameters during March 1991 (Table 2 and Fig. 4). One possible explanation was that diel variation in P-I parameters was suppressed due to the combination of lower temperatures and a shorter photoperiod. Yet another factor may have been the physical conditions affecting the structure of the water column and the extent of mixing. March 1991 was a period of high river discharge (Fig. 2), lower water temperatures, and greater average mixed-layer depth (mean = 9.5 m, SD = 6.6 m, n = 46 in March 1991 compared to mean = 3.2 m, SD = 1.8 m, n = 85 in July–August 1990; slope stations were excluded). Thus, the extent and rate of vertical mixing in March would have led to a variable photic environment that may have obscured diel patterns.

SEASONAL VARIATIONS

Variation in P-I parameters occurred over seasonal time scales (Table 3) that could be partially attributed to variations in temperature (Fig. 5). The exponential relationship observed between high values of P^B_{max} and temperature (Fig. 5) was expected from theoretical considerations (Eppley 1972) and was consistent with previous investigations of estuarine populations (Platt and Jassby 1976; Malone and Neale 1981; Pennock and Sharp 1986; Keller 1989). In fact, the exponential relationship shown in Fig. 5 was virtually identical to
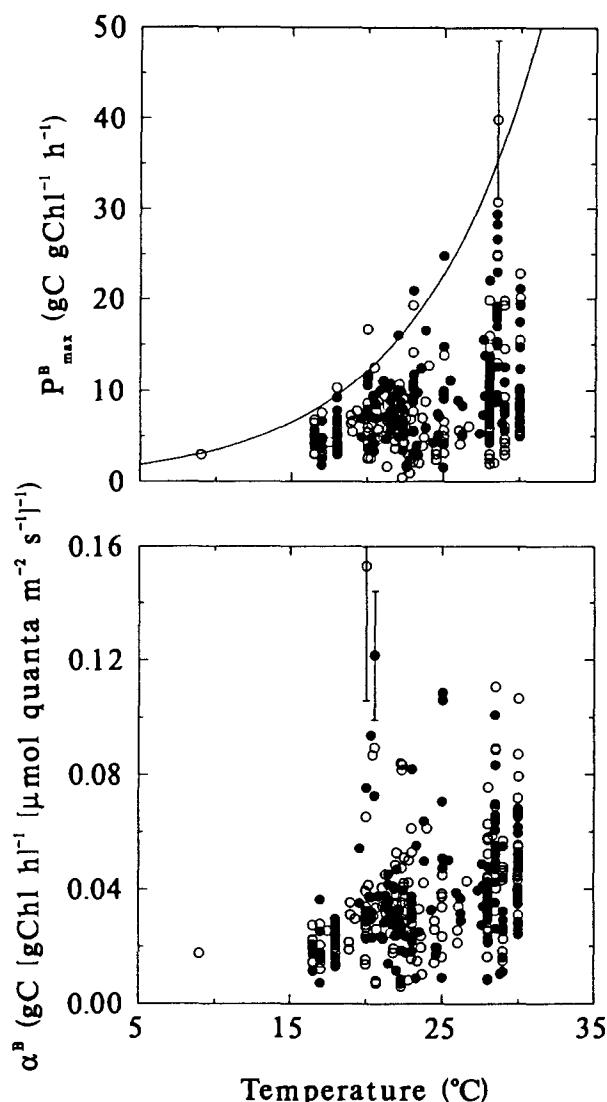

Fig. 5. Combined data for P^B_{max} and α^B from all cruises plotted as a function of temperature (T). Closed symbols indicate results from measurements conducted during midday (1000–1400 hours). Curved line is a subjective fit to the high values and is described by the equation, P^B_{max} = exp(0.125T). P^B_{max} and α^B transformed to their natural logarithms were both significantly correlated with temperature (r^2 = 0.157, p < 0.001, n = 363 for ln[P^B_{max}]; and r^2 = 0.153, p < 0.001, n = 363 for ln[α^B]). Error bars indicate ±1 SE of the estimate and are shown only for the highest values. See text for further discussion.

that observed by Pennock and Sharp (1986) in the Delaware estuary. Both α^B and P^B_{max} were found to be significantly correlated with temperature, although some high values of α^B were encountered at intermediate temperatures (Fig. 5). A significant positive correlation was found between α^B and P^B_{max} for the combined data from all cruises (r^2 = 0.273, p < 0.001, n = 364). This type of correlation has been reported in previous studies (Platt and
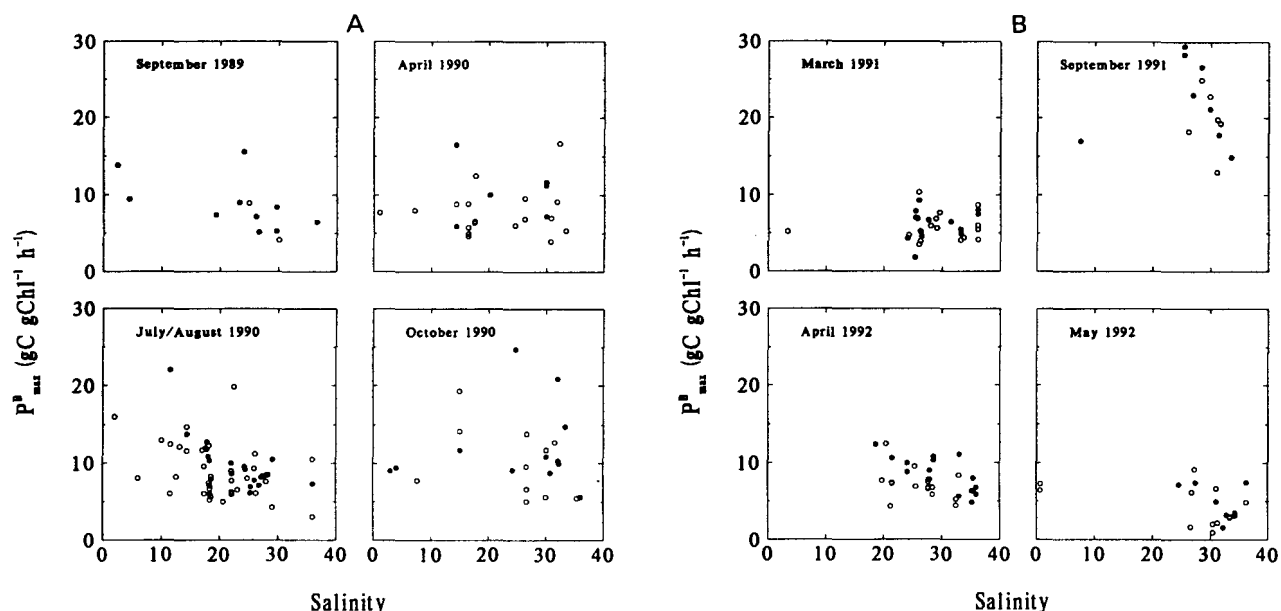
Fig. 6.   Variation in P^B_{max} as a function of salinity. A) Data from September 1989 and April, July–August, and October 1990 cruises; B) Data from March and September 1991 and April and May 1992 cruises. Closed symbols indicate results from measurements conducted during midday (1000–1400 hours).

Jassby 1976; MacCaull and Platt 1977; Harding et al. 1982, 1985). A theoretical basis for covariation of α^B and P^B_{max} can be seen by comparing Eqs. 4 and 5. Both α^B and P^B_{max} will vary as a function of η, the ratio of functional reaction centers to Chl a.

Combining Eqs. 4 and 5 yields the following expression:

$$P^B_{max} = \alpha^B/\sigma\tau \qquad (7)$$

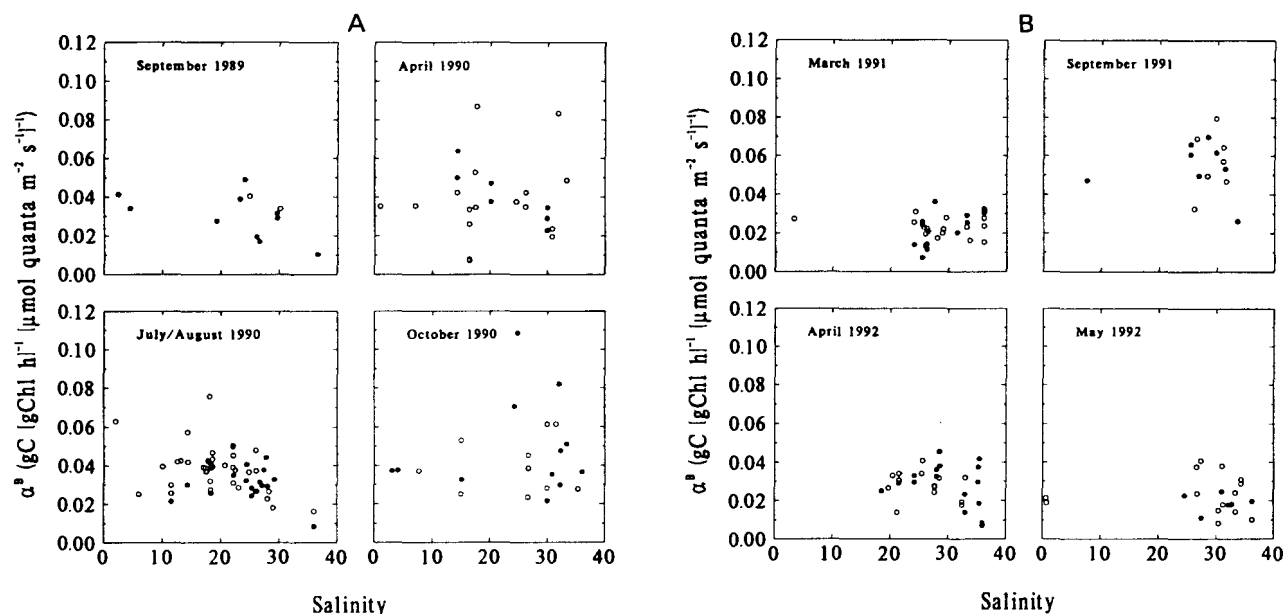From this, it can be seen that the relationship be-

Fig. 7.   Variation in α^B as a function of salinity. A) Data from September 1989 and April, July–August, and October 1990 cruises; B) Data from March and September 1991 and April and May 1992 cruises. Closed symbols indicate results from measurements conducted during midday (1000–1400 hours).
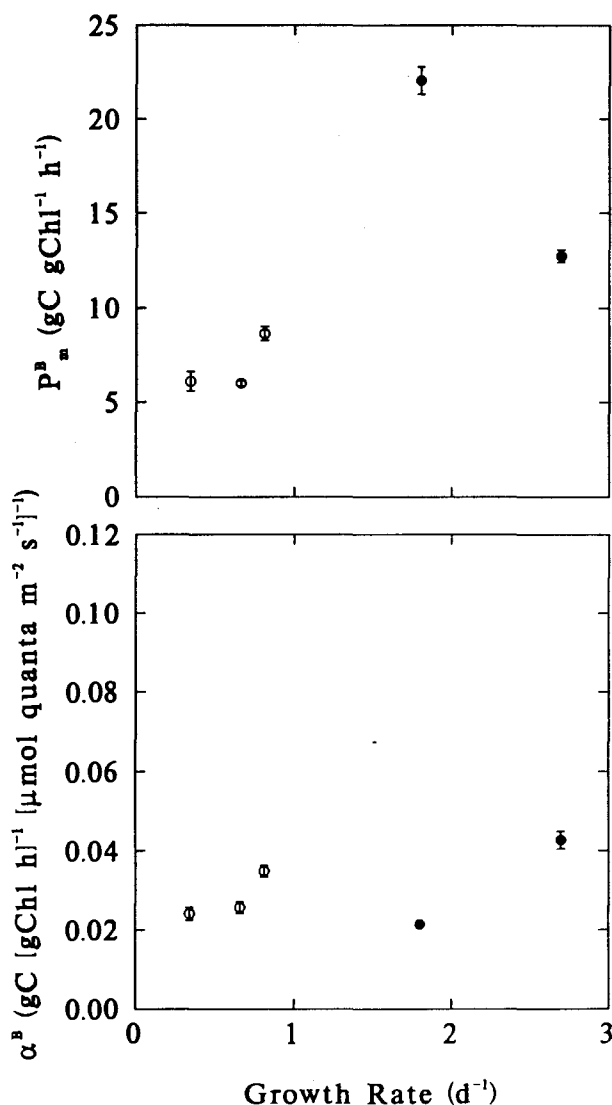
Fig. 8. Relationship of midday (1000–1400 hours) values of P^B_{max} and α^B to growth rate. Filled symbols indicate samples from the plume and open symbols were from shelf waters. Error bars designate ± 1 SE.

data). Hence, the high values of P^B_{max} apparently resulted from a combination of high temperatures and a related shift to smaller phytoplankton species. Various studies have reported higher values of P^B_{max} and α^B in association with smaller cells (Malone 1971a, b; Malone and Neale 1981; Cote and Platt 1983; Platt et al. 1983; Geider et al. 1986).

Some of the values of P^B_{max} observed during September 1991 exceeded the theoretical maximum limit of 25 g C g Chl a^{-1} h^{-1} approximated by Falkowski (1981), although the vast majority of our observed values were below this. Chl a concentrations and associated rates of carbon fixation were quite low during September 1991. As lower limits of detection were approached, measurement errors would have been proportionately larger thus increasing variance and potentially leading to overestimates. Such methodological errors would have been compounded by statistical uncertainties associated with derivation of P-I parameters by nonlinear curve fitting, as illustrated by the error bars in Fig. 5.

A maximum theoretical limit for α^B (cf. Platt and Jassby 1976) can be estimated using the following expression:

$$\alpha^B = \phi_{max} a^* \tag{8}$$

where ϕ_{max} (mol C mol quanta^{-1}) is the maximum quantum yield and a* (m^2 mg Chl a^{-1}) is the spectrally-averaged in vivo absorption cross-section normalized to Chl a. Accepted values for ϕ_{max} generally do not exceed 0.1, while values for a* (sometimes treated as k_c) may range as high as 0.025 depending on spectral composition of irradiance and algal pigment type (e.g., Bannister and Weidemann 1984). An upper limit for α^B would then be 0.0025 mol C (m^2 mol quanta^{-1}) (mg Chl a)$^{-1}$ or 0.11 g C (g Chl a h)$^{-1}$ (μmol quanta m^{-2} s^{-1})$^{-1}$. Again, it can be seen that the majority of our observations fell below this number (Fig. 5). Highest values of α^B were observed during April 1990. That some estimates of α^B were greater than 0.11 during April 1990 may have stemmed from the fact that statistical uncertainties (indicated by error bars in Fig. 5) were greater in some cases for the data from this cruise. This was due to the fact that only nine samples were used to generate each P-I curve in contrast to 18 samples for subsequent cruises.

SPATIAL VARIATION

As in previous studies (Malone et al. 1981; Pennock and Sharp 1986; Fee et al. 1987), we observed a wide range of values below the maximum theoretical limits, suggesting the importance of other controlling factors. Attempts to relate variation in P-I parameters to individual environmental condi-

tween P^B_{max} and α^B will be modified by variations in the product σ_τ (1/I_k) (cf. Cullen 1990).

The range of means of P-I parameters encountered in this study (Table 3) were consistent with values reported for other coastal and estuarine systems (cf. Malone and Neale 1981; Pennock and Sharp 1986). Our highest values of P^B_{max} were observed during the September 1991 cruise, a period of high temperatures and stratified conditions. This majority of phytoplankton primary production was associated with the <8-μm size fraction (Redalje et al. 1994), and populations were dominated by cyanobacteria (Q. Dortch unpublished

TABLE 4. Principal component analyses of environmental variables in the upper mixed layer. Shown are results for the first two principal components, including eigenvalues, percent variance explained by the components, and component loadings for each variable (equivalent to correlations of components with each original variable). n = number of samples, T = temperature (°C), S = salinity, SiO_3^- = silicate (μM), PO_4^{3-} (μM), NO_x = nitrate + nitrite (μM), K = attenuation coefficient (m^{-1}), MLD = mixed layer depth (m), and PAR (daily photosynthetically active radiation at depth, mol quanta m^{-2} d^{-1}). All variables were converted to natural logarithms prior to analysis.

Cruise	Eigenvalues		Percent Variance		Component Loadings			n
	1	2	1	2	Variable	1	2	
September 1989	4.77	2.07	59.6	25.9	T	−0.228	0.958	5
					S	−0.765	−0.478	
					SiO_3^-	0.975	−0.207	
					PO_4^{3-}	0.975	−0.101	
					NO_x	0.979	−0.135	
					K	0.839	0.188	
					MLD	−0.752	−0.094	
					PAR	0.064	0.900	
April 1990	3.94	1.59	65.6	26.5	T	0.916	0.187	7
					S	−0.995	−0.007	
					SiO_3^-	0.921	−0.364	
					NO_x	0.493	−0.821	
					MLD	−0.941	−0.285	
					PAR	0.358	0.817	
July 1990	4.04	1.80	50.5	22.6	T	−0.267	−0.913	14
					S	−0.913	0.080	
					SiO_3^-	0.766	0.065	
					PO_4^{3-}	0.787	0.414	
					NO_x	0.871	0.158	
					K	0.923	−0.243	
					MLD	−0.480	0.582	
					PAR	−0.297	0.606	
October 1990	2.94	1.41	49.1	23.5	T	−0.449	−0.408	7
					S	−0.890	0.340	
					NO_x	0.807	0.268	
					K	0.853	−0.380	
					MLD	−0.736	−0.090	
					PAR	0.171	0.950	
March 1991	3.49	1.61	58.1	26.8	T	−0.710	−0.477	12
					S	−0.901	−0.296	
					SiO_3^-	0.768	−0.435	
					NO_x	0.931	−0.208	
					K	0.711	−0.633	
					PAR	0.459	0.812	
September 1991	3.22	1.16	64.4	23.2	S	−0.758	0.630	6
					SiO_3^-	0.935	0.139	
					K	0.900	−0.100	
					MLD	−0.835	0.006	
					PAR	0.516	0.856	
April 1992	3.41	1.49	56.7	24.8	T	0.090	0.873	13
					S	−0.900	−0.035	
					SiO_3^-	0.923	−0.322	
					K	0.831	−0.328	
					MLD	−0.896	−0.122	
					PAR	0.494	0.708	
May 1992	3.23	1.36	53.8	22.7	T	−0.083	0.753	6
					S	−0.966	−0.185	
					PO_4^{3-}	0.969	0.162	
					NO_x	0.979	0.071	
					K	0.677	−0.237	
					PAR	−0.217	0.820	

TABLE 5. Partial correlation coefficients (with probabilities in parentheses) and squared multiple correlation coefficients from stepwise multiple regression analyses of relationships between principal components and midday values of P^B_{max} and α^B in the upper mixed layer. The principal components served as independent variables and were described in Table 4. r = correlation coefficient, ns = not significant (i.e., predictor probability exceeded 0.15), NA = not applicable.

| | P^B_{max} | | | α^B | | | |
| | Partial r for component | | Multiple r² | Partial r for component | | Multiple r² | |
Cruise	1	2		1	2		n
September 1989	ns	ns	NA	ns	ns	NA	10
April 1990	ns	ns	NA	0.910 (0.004)	ns	0.828	7
July 1990	0.826 (0.001)	0.488 (0.091)	0.758	ns	−0.496 (0.071)	0.246	14
October 1990	ns	ns	NA	ns	ns	NA	7
March 1991	−0.500 (0.098)	ns	0.250	−0.667 (0.018)	ns	0.445	12
September 1991	ns	0.655 (0.110)	0.429	ns	ns	NA	7
April 1992	0.880 (0.001)	ns	0.774	ns	−0.508 (0.064)	0.258	14
May 1992	ns	ns	NA	ns	−0.784 (0.065)	0.615	6

tions were complicated by the fact that many environmental variables were correlated. Principal component analysis was used to derive independent component variables that described the majority of variation in the environmental data for the mixed layer. The analysis provided information about the pattern of variation of individual variables in relationship to one another, and the manner in which the variation was partitioned among variables. As was expected, the largest portion of the variation, as described by the first principal component, was associated with changes along the salinity gradient (Table 4). The first principal component showed a strong negative association with salinity and positive associations with nutrients, reflecting the high inputs of riverine nutrients and decrease in concentrations along the salinity gradient. Similarly, attenuation coefficient was positively associated with the first component due to the high turbidity associated with river outflow, while mixed layer depth was generally negatively associated with the first component as it showed a tendency to increase with increasing salinity. A smaller proportion of the variation was accounted for by the second principal component, which dis-

played a positive association with daily PAR and was weakly related to salinity. The lack of a strong correlation between daily PAR and salinity may have been a consequence of the fact that sampling depths were adjusted according to light levels. The relationships of variables to the principal components were quite similar for all cruises, evidence that the observed patterns were persistent and real, rather than transitory or a consequence of chance variation in random data.

The principal component analysis yielded independent variables in the form of principal components that described the majority of environmental variation, and these component variables were then related to P-I parameters using stepwise multiple regression techniques. Relationships between P-I and principal component variables were significant in some cases (Tables 5 and 6). Correlations with the first principal component were an indication that spatial variability in P-I parameters was related to river outflow. For example, positive correlations of P^B_{max} with the first principal component during July–August 1990 and April 1992 were consistent with observations of higher midday values of P^B_{max} at lower salinities (Fig. 6). Both

TABLE 6. Partial correlation coefficients (with probabilities in parentheses) and squared multiple correlation coefficients from stepwise multiple regression analyses of relationships between principal components and midday values of I_k in the upper mixed layer and for all depths. Principal components served as independent variables and were described in Table 4 (mixed layer) and Table 7 (all depths). r = correlation coefficient, ns = not significant (i.e., predictor probability exceeded 0.15), NA = not applicable.

| | Mixed Layer | | | | All Depths | | | |
| | Partial r for component | | Multiple r² | n | Partial r for component | | Multiple r² | n |
Cruise	1	2			1	2		
September 1989	−0.821 (0.088)	ns	0.674	5	−0.789 (0.007)	0.558 (0.118)	0.740	10
April 1990	−0.679 (0.094)	ns	0.461	7	ns	−0.582 (0.077)	0.339	10
July 1990	ns	0.679 (0.008)	0.461	14	−0.418 (0.019)	−0.365 (0.056)	0.285	29
October 1990	ns	ns	NA	7	−0.617 (0.025)	ns	0.381	13
March 1991	ns	ns	NA	12	−0.580 (0.006)	ns	0.336	21
September 1991	ns	0.635 (0.125)	0.404	7	−0.721 (0.001)	0.388 (0.091)	0.592	21
April 1992	ns	0.590 (0.026)	0.348	14	−0.609 (0.001)	0.288 (0.145)	0.423	28
May 1992	ns	0.706 (0.117)	0.498	6	−0.443 (0.150)	0.555 (0.040)	0.444	13

TABLE 7. Principal component analyses of depth, temperature, and PAR variables for all depths sampled. Shown are results for the first two principal components, including eigenvalues, percent variance explained by the components, and component loadings for each variable (equivalent to correlations of components with each original variable). n = number of samples, T = temperature (°C), Depth (m), and PAR (daily photosynthetically active radiation at depth, mol quanta m^{-2} d^{-1}). All variables were converted to natural logarithms prior to analysis.

| Cruise | Eigenvalues | | % Variance | | Component Loadings | | | |
	1	2	1	2	Variable	1	2	n
September 1989	2.35	0.424	78.3	14.1	Depth	0.877	0.410	10
					T	−0.853	0.500	
					PAR	−0.923	−0.072	
April 1990	2.33	0.521	77.6	17.4	Depth	0.940	0.181	10
					T	−0.792	0.609	
					PAR	−0.905	−0.344	
July 1990	1.78	1.01	59.5	33.6	Depth	0.932	−0.176	29
					T	0.144	0.988	
					PAR	−0.947	−0.023	
October 1990	2.27	0.556	75.5	18.5	Depth	0.903	−0.322	13
					T	0.770	0.637	
					PAR	−0.926	0.216	
March 1991	2.08	0.747	69.5	24.9	Depth	0.935	−0.193	21
					T	0.638	0.769	
					PAR	−0.897	0.345	
September 1991	2.09	0.803	69.8	26.8	Depth	0.935	−0.276	21
					T	0.567	0.823	
					PAR	−0.948	0.221	
April 1992	2.21	0.612	73.7	20.4	Depth	0.906	0.308	28
					T	−0.734	0.679	
					PAR	−0.923	−0.237	
May 1992	1.71	1.00	57.1	33.4	Depth	0.926	−0.008	13
					T	−0.099	0.994	
					PAR	−0.920	−0.115	

P^B_{max} and α^B were negatively correlated with the first principal component in March 1991. This apparent seasonal shift in relationships between P-I parameters and river outflow could be explained by low temperatures in the river. A negative association between temperature and the first principal component in March 1991 indicated cooler temperatures at lower salinities.

Horizontal variations in P^B_{max} in July–August 1990 reflected trends in growth rate (Fig. 8), possibly related to increasing nutrient limitation with distance from the river plume. The changes in growth rate were proportionately larger than changes in P^B_{max}. Variations in carbon to Chl a ratios (g g^{-1}), ranging from 12 in the plume to 125 on the shelf (Lohrenz et al. 1992a; Redalje et al. 1994), would tend to moderate growth-rate-dependent changes in P^B_{max} (cf. Falkowski 1981; Cullen 1992). In addition to physiological changes within species populations, changes in species composition may have

TABLE 8. Partial correlation coefficients (with probabilities in parentheses) and squared multiple correlation coefficients from stepwise multiple regression analysis of relationships between prinicipal components and midday values of P^B_{max} and α^B for all depths sampled. Principal components served as independent variables and were described in Table 7. r = correlation coefficient, ns = not significant (i.e., predictor probability exceeded 0.15), NA = not applicable.

| Cruise | P^B_{max} | | | α^B | | | |
| | Partial r for component | | Multiple r^2 | Partial r for component | | Multiple r^2 | n |
	1	2		1	2		
September 1989	−0.795 (0.004)	−0.552 (0.123)	0.744	ns	0.757 (0.011)	0.573	10
April 1990	ns	ns	NA	ns	0.565 (0.089)	0.319	10
July 1990	−0.387 (0.038)	ns	0.150	ns	ns	NA	29
October 1990	−0.505 (0.079)	ns	0.255	ns	ns	NA	13
March 1991	ns	0.504 (0.020)	0.254	0.574 (0.005)	0.364 (0.115)	0.418	21
September 1991	−0.665 (0.001)	0.520 (0.019)	0.593	ns	ns	NA	21
April 1992	−0.499 (0.007)	ns	0.249	0.385 (0.043)	ns	0.148	28
May 1992	ns	ns	NA	ns	−0.443 (0.129)	0.196	13

influenced observed spatial patterns in P-I parameters. Redalje et al. (1992, 1994) found a larger proportion of primary production associated with the smaller size fractions (<8 μm) in plume waters as compared to shelf waters during July–August 1990. As mentioned previously, higher values of P^B_{max} and α^B would be expected for smaller cells. While this was consistent with the trends we observed in P^B_{max}, we found no significant regional differences in α^B in July–August 1990, nor was the relationship between α^B and μ significant (Fig. 8). Under conditions of increasing nutrient limitation in phytoplankton cultures, σ has been observed to increase and η decrease (Kolber et al. 1988; Falkowski 1992). From Eq. 5, it is apparent that these changes would have opposing influences on α^B. There was statistical evidence of regional differences in $1/\sigma\tau$ (= I_k) (Fig. 3), although there was considerable overlap in observed ranges of values. An increase in the product, $\sigma\tau$, in regions of lower growth rate could be expected as both σ and τ have been observed to increase with increasing nutrient limitation in phytoplankton cultures (Kolber et al. 1988; Falkowski 1992).

VARIATION IN RELATIONSHIP TO PAR AND DEPTH

Information about relationships of P-I parameters to variations in daily PAR was provided in two ways. First, the second principal component in Table 4 showed a consistent positive association with daily PAR. Observed correlations with P-I parameters were consistent with expectations about relationships between PAR and P-I parameter variation (cf. Falkowski 1981; Cullen 1990). Positive correlations were observed between this principal component and P^B_{max} (Table 5) and I_k (Table 6), and negative correlations were observed with α^B (Table 5). The variation in PAR described by the second principal component was not attributable to variation in attenuation coefficient, as this was most closely related to the first principal component in Table 4. Prior investigations in the Chesapeake Bay (Harding et al. 1985) and the Delaware estuary (Pennock and Sharp 1986) found no significant relationship between attenuation coefficient and P-I parameters in mixed-layer populations. Such a result is understandable since mixed-layer populations would likely experience variable irradiance due to mixing across the vertical light gradient over the course of the photoperiod, particularly in turbid plume environments. It is also evident from the principal component analysis of mixed-layer data in Table 4 that several other environmental variables covaried with attenuation coefficient (i.e., first principal component), and these other variables could also influence P-I parameters.

A second approach that provided information about relationships between P-I parameters and daily PAR initially involved principal component analysis of depth, daily PAR at depth, and temperature variables. This revealed that the majority of the variation in daily PAR was related to depth in the first principal component (Table 7). For midday data from several cruises, P^B_{max} (Table 8) and I_k (Table 6) were found to be inversely related to the first principal component, from which was inferred an inverse relationship with depth and positive association with daily PAR. Temperature showed both negative and positive associations with the first principal component (Table 7), and thus potentially reinforced or suppressed the vertical gradients in P-I parameters. Variations in α^B were found to be positively correlated with the first principal component in March 1991 and April 1992 (i.e., varied inversely with daily PAR along vertical gradients) (Table 8). Responses of P-I parameters to changes in irradiance depend on the time scales and direction of shift in irradiance (e.g., Falkowski 1984; Neale and Marra 1985; Cullen and Lewis 1988). An important factor in explaining vertical patterns may be the relationship between the rate of mixing and rate of photoadaptation (Cullen and Lewis 1988). Slower mixing rates would potentially result in higher near-surface values of P^B_{max} and more distinct vertical gradients in both P^B_{max} and α^B. This possibility should be examined in future studies.

Conclusions

Our results indicate that relationships between P-I parameters and environmental conditions in our study region were significant in some cases, but variations between cruises made it difficult to generalize. While it is possible to account for some of the variation in P-I parameters on the basis of conditions during a specific period, no simple rules exist for predicting a priori the values of P-I parameters. This was partially due to the fact that many environmental variables were correlated, thus complicating the identification of causative factors. Another element contributing to the apparent complexity in P-I parameter variation was that changes in physiological variables (i.e., μ, C:chl, η, τ, and σ) were often the result of changes in species composition as well as physiological changes within species populations. Indeed, in the northern Gulf of Mexico, spatially distinct phytoplankton populations occur in river, plume, and shelf waters (Dortch et al. 1992; Fahnenstiel et al. 1992). Given the current state of knowledge, there appears to be no substitute for direct observation of P-I parameters. However, our findings do support the view that a limited set of observations may be ad-

equate to characterize a given region within a restricted period of time. The implications of the observed variation in P-I parameters for the predictability of primary production using regional scale bio-optical algorithms will be examined in a subsequent paper (Lohrenz et al. in preparation).

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